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GROWTH PROCESSES IN THE POSTEMBRYONIC DEVELOPMENT IN ALTRICIAL BIRDS ON THE EXAMPLE OF SONG THRUSH, *TURDUS PHILOMELOS* (PASSERIFORMERS, TURDIDAE): A MULTIVARIATE APPROACH

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Growth Processes in the Postembryonic Development in Altricial Birds on the Example of Song thrush, *Turdus philomelos* (Passeriformes, Turdidae): a Multivariate Approach. Peskov, V. N., Franchuk, M. V., Atamas', N. S. — The paper explores the possibility of implementing the methods of multivariate statistics into studying the growth processes on the example of song thrushes, *Turdus philomelos,* Brehm, 1831, during their postnatal development as nestlings. The developmental trends in 12 morphometric traits in *T. philomelos* in the course of postembryogenesis is shown to be explained for 99.3 % by the first two principal components (PC). The major developmental trend (PC_1 — 95.1 %) is defined by a highly correlative though irregular growth of linear forms of nestlings' body parts, the two other trends relate to the body proportion formation (PC_2 — 4.2 %). There have been discovered the two growth stages: (1) of fast growth: from birth up to the 8th day with relative increment in growth of traits equal in average to 91.9 %, and (2) of slow growth: from the 8th to the 14th day, characterized by a reduction of an average growth increment being five times lower, and by intense feather cover development. There have been demonstrated that all the variables can be structured into the four groups or growth correlation pleiads (groups comprising similarly growing traits). The growth is shown to be most specific for the song thrush's body, head and bill, being a part of a singl e pleiad. While still forming the three different growth pleiads the properties of the bird's wing, leg, the 3rd and the 4th toes differ significantly less in respect to their growth characteristics.
K e y w o r d s*:* song thrush, postembryonic growth, growth phases, developmental trends, multivariate analysis.

Ростовые процессы в постэмбриональном развитии птенцовых птиц на примере певчего дрозда, *Turdus philomelos* (Passeriformes, Turdidae): многомерный подход. Песков В. Н., Франчук М. В., Атамась Н. С. — На примере певчего дрозда, *Turdus phillomelos,* Brehm, 1831, анализируются возможности изучения ростовых процессов в постэмбриональном развитии птенцовых птиц с использованием методов многомерной статистики. Показано, что изменчивость 12 морфометрических признаков в постэмбриогенезе *T. phillomelos* на 99,3 % описывается первыми двумя главными компонентами (ГК). Основной тренд изменчивости признаков ($ГК_1$ — 95,1 %) определяется высоко согласованным, но неравномерным увеличением линейных размеров частей тела птенцов, два других тренда связаны с формированием его пропорций ($ГК_2$ — 4,2 %). Выявлены фаза интенсивного роста (с 0 до 8 суток, относительный прирост признаков в среднем составляет 91,9 %) и фаза замедленного роста (8–14 суток, характерно уменьшение величины среднего относительного прироста в 5 раз, интенсивное развитие перьевого покрова). Показано, что по величине суточного прироста и характеру динамики ростовых процессов все признаки объединяются в 4 группы или ростовые плеяды (группы одинаково растущих признаков). Наиболее специфично растут тело, голова и клюв, образующие единую плеяду. Признаки крыла, ноги, третьего и четвертого пальцев, хотя и образуют три отдельные ростовые плеяды, различаются по характеристикам ростовых процессов значительно меньше.

К л ю ч е в ы е с л о в а*:* певчий дрозд, постэмбриональный рост, фазы роста, тренды изменчивости признаков, многомерный анализ.

Introduction

Postembryonic growth and development of altricial birds has been thoroughly examined to date, as evidenced by numerous studies encompassing both general and specific research on various aspects of avian development (e. g. see Mal'chevsky, 1959; Poznanin, 1979; Rodimtsev, Konstantinov, 2006; O'Connor, 1984; Ricklefs, 1968, 1983). In most of these studies analysis is more concerned with the general growth of the whole organism (body mass and length) than with growth of its parts and organs. In particular in the papers of foreign authors, body weight shifts are considered to be the main characteristic of a growing organism far more frequently than correlated trends for separate body parts and organs (Dunn, 1975; Ricklefs, 1967, 1968, 1979; O'Connor, 1978). Phylogenetic and ecological aspects of an organism's growth are given preference in the studies (Becker, Specht, 1991; Bryant, 1978; Coulter, 1981; Dawson, Evans, 1960; Hébert, Barclay, 1986; Lilja, 1982; O'Connor, 1978; Ricklefs, 1967, 1975). However, the correlated dependencies between the developing structures of the organism's organs and body parts in relation to their significance in organism's holistic vital activity (ecology) were not paid enough attention in the research literature in the past. There are hardly any studies on correlative relationships between body parts and organs of the developing organism (O'Connor, 1978; Peskov, 1990; Peskov et al., 2013). Although according to Poznanin's opinion (1979), this approach would allow us to understand the mechanisms of the body proportion formation as conditioned by specific connections between the organism and its environment.

Based on the facts referred above, the main aim of this study was to identify the most important signs of integrity of the growing organism in the postembryogenesis of altricial birds using multivariate statistics methods.

Material and methods

Place of data collection. In our study we used the research data on breeding biology of the song thrush. The data were collected in June 2012, in natural object "Razvylka" (near Sarny, Rivne Region), Rivne Natural reserve (the Biloozersky and Somyne areas near Yarynivka village, Sarny District of Rivne Region) and near Poliana village, Shepetovsky District of Khmelnytcky Region. The area of research is located in the mixed forests of Ukrainian West Polissia.

Data. There have been studied 118 nestlings of different age in total and 15 adult birds. Nestlings of 1 to 14 days of age were measured with digital calipers. Each nestling was measured regularly with a two-day period since hatching till leaving the nest.

The analyzed traits included: 1) *body length* — the distance (with the neck extended) from the bill point to coccyx (feathers not counted); 2) *head length* — the distance from the back of head to the bill tip; 3) *total bill length (survey 1)* — the distance from the bill's tip to the edges of ramphotheke and skin cover of the frontal area; 4) *bill length from the tip to the nostrils (survey 2)* — the distance from the bill tip to the nostrils; 5) *shoulder length* — the distance from the middle of shoulder joint to the middle of the elbow; 6) *forearm length* — the distance from the middle of the elbow to the middle of the carpal joint; 7) *wingtip length* — the distance from the middle of carpal joint to the distal edge of the wingtip; 8) *thigh length* — the distance from the middle of hip joint to the middle of knee joint; 9) *tibia length* — the distance from the middle of knee joint to the middle of intertarsal joint; 10) *tarsus and foot length* — the distance from the middle of intertarsal joint to the toe joint (with toes bent); 11) *third (the longest) toe length* — the distance from the base of the middle toe joint of foot to the emerging claw; 12) *fourth toe length* — the distance from the base of toe joint of foot to the emerging claw (Poznanin, 1979, with corrections).

The original surveys were used to calculate: 13) head length without bill; 14) shoulder and forearm length; 15) forearm and wingtip length; 16) total wing length; 17) thigh and tibia length; 18) tibia and tarsus length; 19) total leg length; 20) fourth and third toe length.

Statistical methods. For every age group of nestlings the means of measured values were calculated, which were further analyzed in the study of growth development. The variability of morphological traits in postembryonic development of the song thrush was studied using principal components analysis. The growth of the whole body and its different parts was estimated by the relative percentage increment (RPI, %), calculated according to Brody's formula (Schmalhausen, 1982). Hierarchical cluster analysis was implemented to compare all the twenty traits by their diurnal relative percentage increment (DRPI, %). The differences were calculated by means of Euclidean squared distance metric (SqDE), with implementation of Spearman rank correlation coefficient (RS) for the analysis of growth dynamics (variations in DRPI, %) Data processing and analysis were conducted with the help of Microsoft Office Excel and Statsoft Statistica 6.0.

Nestlings and their parents had been treated so that to maximally reduce any unfavorable effects on them. No nestlings during the measurement procedures had been harmed.

Results and discussion

Component analysis of ontogenetic developmental trends. According to the analysis results (table 1) the first two principal components describe developmental shifts for the 12 morphometric traits in the sample of nestlings, fledglings

Table 1. Factor loadings for two first principal components (PC_1 and PC_2)

No.	Traits, mm	PC_1	PC_2
1	Body length	–0.991	0.091
2	Head length	–0.984	0.170
3	Total bill length	–0.941	0.328
4	Bill length from the tip to the nostrils	–0.927	0.374
5	Shoulder length	–0.996	0.005
6	Forearm length	–0.976	–0.202
7	Wingtip length	–0.968	–0.249
8	Thigh length	–0.989	0.101
9	Tibia length	–0.994	–0.072
10	Tarsus and foot length	–0.975	–0.210
11	Third toe length	–0.969	–0.221
12	Fourth toe length	–0.990	–0.092
Prp. totl., %		95.10	4.20

and adult song thrushes (99.3 % of total variance). Negative sign and high values of factor loadings on the first component attest to their tightly coordinated changes in the course of postnatal development.

Biological nature of these changes is quite obvious. The first principal component (PC_1) that explains 95.1 % of total variance, characterizes age-related changes in the linear size of the body and its parts. Thus, coordinated increment in all the traits in the postnatal development of song thrush nestlings should be interpreted as the main "growth trend". Negligible differences in values of the calculated factor loadings of different traits on PC_1 signify that changes are irregular (allometric growth) which is characteristic for the body proportion formation in nestlings.

PC_2 (3.10 % of total variance) characterizes different growth vectors in the traits as they relate to each other, i.e. the formation of body proportions. It is evident from the value and sign of factor loadings for PC_2 (table 1). For example, low positive factor loadings of body, head, bill and thigh lengths mean that there is an independent developmental trend which is though aligned with the main trend (PC_1), determined by growing body linear metrics in nestlings during their nesting period of development. Negative loadings for forearm, wingtip, tarsus and foot, third toe, forearm and wingtip, tibia and tarsus, third and four toes' lengths indicate that there is a specific developmental trend for the traits, partly independent from the main 'growth trend'.

Factor analysis of the growth processes. Considering that PC_1 and PC_2 explain 99.3 % of song thrush's postnatal developmental trends in respect to the described 12 traits, the factor scores of these components carry similarly meaningful information about the changes in the body linear sizes (PC_1) and body proportions (PC_2). Having connected these values (dots) in the graph (fig. 1) with a broken line, we can observe a schematic trajectory representing the postembryonic development of song thrush's body in a multivariate space.

Judging by figure 1, there is an irregular increment of linear body metrics in the song thrush's postembryonic development. For instance, since hatching till the 8th day nestlings rapidly grow (phase of rapid growth). The mean value of RPI for the 20 traits equals 91.9 %. From the 8th day till leaving the nest (at the 13th–14th day) the rates of linear growth drop considerably (phase of slow growth). The mean RPI value is reduced by almost 10 times and makes up 9.56 %. Such a big size increment drop for the axial and limb skeletons of nestlings is definitely a result of the processes of intense growth and feather cover differentiation (Mal'chevsky, 1959; Bel'sky, 1960; O'Connor, 1978; Poznanin, 1979; our own data). Similar relation between the processes of growth and differentiation was found by Bel'sky (1960) for snowbird and some other bird species.

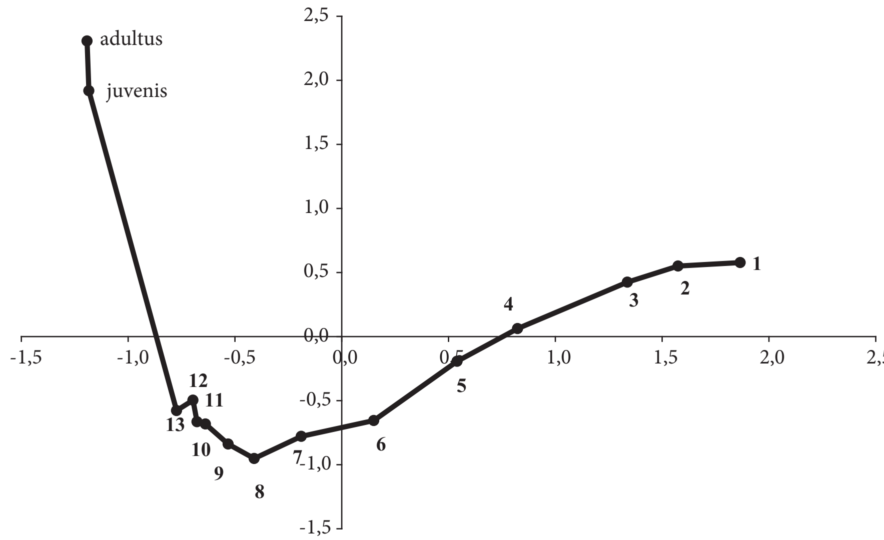


Fig. 1. Distribution of centroids for the age-based song thrush samples in the factor space of PC_1 and PC_2 (figs 1–13 denote nestling's age in days).

The trait-related structure of growth processes can be clearly seen in figure 2. During the phase of rapid growth (0–8 days) wings demonstrate the most prominent growth increment (103.1 %) together with almost all its parts (RPI is maximal for forearm: 110.3 %, and minimal for wingtip: 99.0 %). The second-largest RPI is found for legs and is maximal for tarsus (107.3 %) and the third toe (107.3 %), and minimal for thighs (87.0 %). The third place was shared among bill (77.4 and 75.5 %, respectively), body (66.4 %), head with bill (59.8 %) and head without bill (49.8 %). The main task to be solved by the nestling's organism in the phase of intensive growth is the maximal increase in the linear size of the body and formation of its definitive proportions.

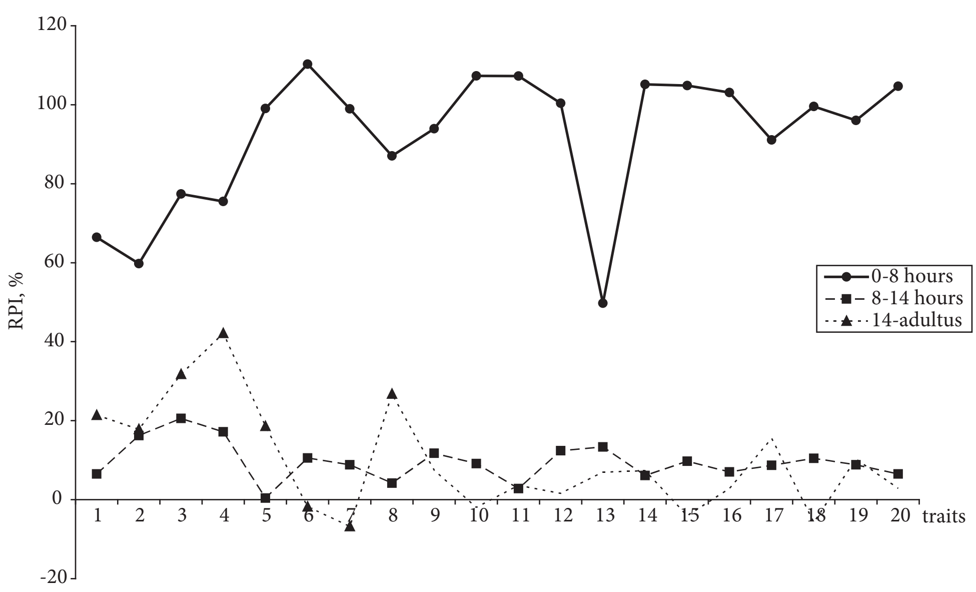


Fig. 2. RPI values for 20 traits during the phase of rapid growth (0–8 days), phase of slow growth (8–14 days) and after leaving the nest (14 days to adulthood). Numbers of traits as given in table 1.

Between the 8th and the 13th–14th days (phase of slow growth), the body's linear size continues to increase though at a much slower pace (fig. 2). Of interest is that the bird's head and bill in particular are growing significantly faster than its wings and legs. The maximal RPI value is observed for bill (20.6 % and 17.2 %), head with bill (16.2 %) and head without bill (13.4 %). Minimal RPI is demonstrated by thigh (4.2 %) and the third toe (2.8 %), while the fourth tow significantly adds in size (12.4 %). Shoulders stop their growth almost completely (0.38 %). These and some other growth indices denote the final stage of a nestling's development before it is ready to leave the nest.

After leaving the nest by the 13th–14th days, nestlings continue to grow until they reach the size of an adult bird. During that period, their bills elongate from tip to nostrils for 42.1 % and for 31.7 % in total, which is undoubtedly a result of a transition to feeding by their own. Size increments of 26.8 % for thigh and 15.5 % for thigh and tibia together obviously reflect the heightened locomotor activity related to the search for food. These are the indications that a nestling is about to get ready for an independent living.

Conjugated trait growth in postnatal development of song thrush nestlings. Comparing the traits by their diurnal relative percentage increment (DRPI values) and by the dynamics of the growth processes (sequential increases and decreases in DRPI) we have found that all of them are clearly divided into 4 groups (fig. 3).

There have been demonstrated that all the variables can be structured into the four groups, or growth correlation pleiads (the term is used to signify the groups of identically growing traits).

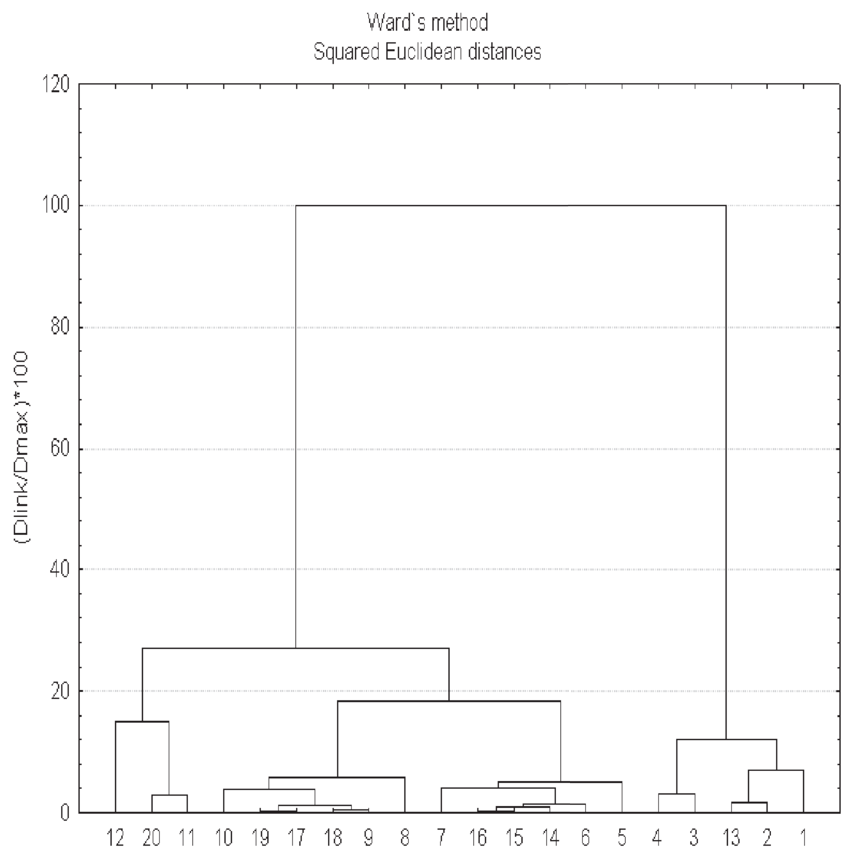


Fig. 3. Results of comparison of 20 morphometric traits (1–20) in nestlings of song thrush according to their DRPI and dynamics of growth processes. Numbers of traits as given in table 1.

However, the main differences between the traits are mostly determined by their DRPI values and to a lesser extent by the dynamics of the growth processes (fig. 4).

The data in figure 3 demonstrate that in postnatal development of song thrush nestlings, their bodies, heads and bills (No. 1, 2 and 13, 3 and 4 respectively) show the most specific growth dynamics of all the examined traits. This conclusion is supported by the results of the growth processes study in nestlings, discussed above. The differences between the growth traits regarding wings and legs are not as significant, as the traits dealing with body, head and bill, although sufficient enough to separate them into different growth pleiads.

It is also important to note that all the traits increase rhythmically. The rhythmic character of the growth processes of vertebrates had already been described before by Schmalhausen (1982). Growth rhythm (dynamics) of the body and its parts in song thrush nestlings can be easily traced throughout the whole nesting period of song thrush development, but most clearly is expressed in the first 8 days, i.e. in the phase of intense growth. The effect of slowing growth rhythms can be observed in line with the decrease in growth rate of nestlings (fig. 4).

Conclusions

The variability of morphometric traits in song thrush's postembryonic development is for 99.3 % explained by the first two principal components. At the same time, high factor loadings of PC_1 for all the 20 analyzed traits (96.2 % of total variance) point out to the very high coherency of their growth. Thus, correlated increment in size of the body and its parts can be seen as a "growth trend" in the whole variance of corresponding traits.

PC_2 (3.1 %) has light positive factor loadings for body, head, bill, and thigh lengths, which indicates the existence of an independent developmental trend, that matches by sign with the main developmental trend for all the traits (PC_1). Negative factor loadings of forearm, wingtip, tarsus, third and fourth toe lengths are also pointing out to a separate independent developmental trend in the above mentioned traits, which can be determined by their slightly lagging growth.

During the nesting period of song thrush development there are a clearly defined phase of rapid growth (0–8 days) and a phase of slow growth (8–14 days). During the

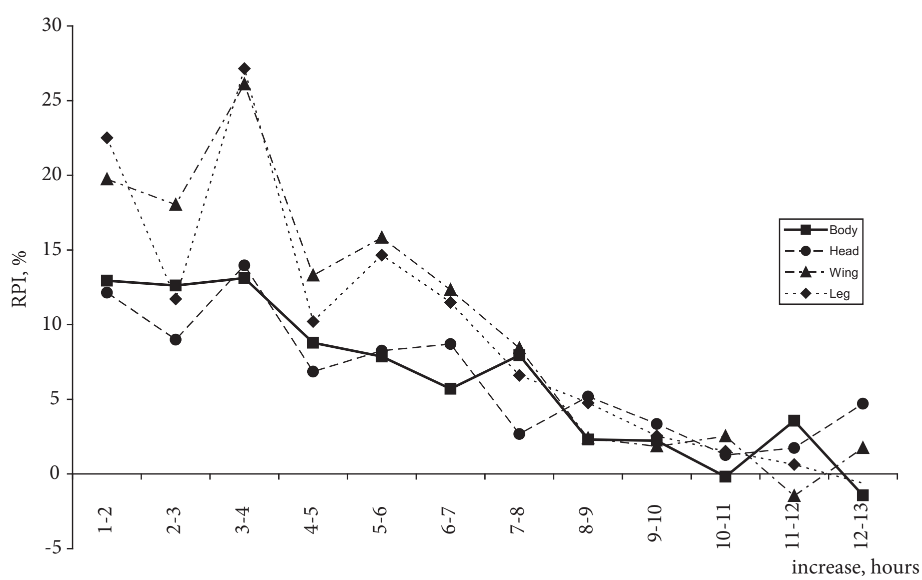


Fig. 4. Dynamics of DRPI values of body, head, wing and leg in the breeding period of song thrush nestling development.

intense growth phase, the trait linear sizes are increased by 91.9 % in average. In the next phase, the average value of RPI is reduced by almost 10 times, and amounts to 9.6 %. In the period after leaving the nest and before reaching maturity the average value of RPI reaches 9.8 %.

During the rapid growth phase (0–8 days), the linear sizes of the nestling's body go through the maximum increase stage and the body's definitive proportions are being formed. In the phase of a slow growth (8–13–14 days) nestlings go through the final stage of their development before they are ready to leave the nest. Their growth dynamics after leaving the nest is being determined so as to ensure a successful transition to independent living.

All the 20 traits can be clearly structured into the four groups, or growth correlation pleiads according to their values of diurnal relative percentage increment (DRPI) and the dynamic nature of the growth processes (sequential DRPI increases and decreases). The growth is shown to be most specific for the song thrush's body, head and bill, being a part of a single pleiad. While still forming the three different growth pleiads, the properties of the bird's wing, leg, the 3rd and the 4th toes differ significantly less in respect to their growth characteristics.

We can assume that in the postembryonic development the nestling's body and all its parts grow rhythmically. It is most clearly expressed in the first 8 days of development (phase of intense growth). As the relative increment of traits slows down, these rhythms appear to fade.

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